15.

On the Color Changes of Fiddler Crabs (Genus *Uca*) in the Field.[1]

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[This is a contribution resulting from a trip ade in the spring of 1944 to Venezuela, lombia and Ecuador, under the auspices of e New York Zoological Society and the Comttee for Inter-American Artistic and Inlectual Relations. Invaluable assistance was ceived from Dr. William Beebe, Director of e Department of Tropical Research, the Creole troleum Corporation, Mr. and Mrs. William H. elps and Mrs. Sherman P. Haight.]

CONTENTS.

I. INTRODUCTION.

During the past few years a number of estigators have done a great deal of cellent experimental work on the role of retions from the crustacean eyestalk us gland and central nervous organs in romatophore activation. Fiddler crabs ve been frequently employed with great ccess as the subjects of the experiments. ne of this research, however, by its very ture could be done on animals living in tural surroundings, and all was performed three western Atlantic species, *Uca pugx, U. minax* and *U. pugilator,* none of ich shows the high degrees of color deopment found in some tropical forms ring display. Our own previous observans (1941, 1943.1, 1943.2) indicated both importance of the natural habitat in nging about the crab's most extreme or changes and the great diversity of or development within the genus. Therefe it seems worthwhile to present certain re recent observations, summarize the field color studies, and correlate these as much as possible with the results of the laboratory investigators. By this means it is hoped that directions will be suggested for future research, preferably in ideal combinations of experimental endocrinology with observation in the field. My thanks go to Dr. F. A. Brown, Jr., for his helpful comments via personal letter on some of his unpublished observations.

Kleinholz (1942) and Brown (1944) have published the most recent and comprehensive surveys of our present knowledge of crustacean hormones, including the mechanism of chromatophore control. For detailed discussion of the subject and extensive bibliographies, reference should be made to these papers. For the purposes of this discussion, the following brief résumé may be made of the aspects immediately related to the present subject.

A. *Brachyuran Chromatophores:* It is known that in brachyuran crabs most external pigment is located in monochromatic chromatophores which are found chiefly in the epidermis. They have permanent branching processes, so that the pigment may be either concentrated in the chromatophore's center, in which case it is scarcely or not at all perceived in the macroscopic coloration of the crab, or it may be widely dispersed into the processes. Four pigments occur in crab chromatophores, all of which are found in *Uca*: black or brownish-black (probably a melanin; hereafter called simply "black"), red, yellow and white (perhaps guanin). A fifth crustacean pigment, a blue, is the only one found outside of the chromatophores; it has not been investigated in *Uca*, although blue is of frequent occurrence in the genus.

All of the striking specific color differences noted when fiddler crabs are studied in the field may be explained by the assumption that each species contains these five pigments in varying proportions, distribution and states of dispersal. Research, however, has scarcely begun on this question: Carlson (1936, p. 67), working with *pugilator,* found red chromatophores fewest of all

[1] ntribution No. 695, Department of Tropical Research, York Zoological Society.

kinds, but still numbering half as many as the abundant black; Abramowitz (1937) found, on the other hand, that in *pugnax* red is usually lacking. A connection between localized white chromatophores and breeding condition has been demonstrated in female shrimps (*Leander*) (Knowles & Callen, 1940), and similar seasonal influences will almost certainly be found to apply to some pigments in *Uca*. Doubtless there will prove to be differences of specific rank in amount or potency of hormones affecting the dispersal of pigments, of importance equal to or greater than the actual number of chromatophores or amount of pigment within them. At present, however, nothing whatever is known of these aspects.

B. *Hormonal Activators of Chromatophores in* Uca: Two sources of chromatophorotropic hormones are at present known to exist in fiddler crabs, the sinus gland of the eyestalk and the central nervous organs. The hormonal principles in the sinus gland, numbering at least two, are responsible for the dispersal of the black, red and perhaps the white chromatophoral pigment, and the concentration of the yellow and perhaps the white. One or more principles from the central nervous organs bring about the dispersal of both the black and the white, as in the case of the sinus gland, according to an unpublished paper by Brown & Cunningham (Brown, 1944, p. 131, and personal communication). The known effects in *Uca* may be expressed in Table 1. The influence of hormones on the blue, probably extrachromatophoric, pigment is omitted because of lack of data.

TABLE I. CHROMATOPHORE CONTROL IN UCA.

Origin of Hormone (s)	*Effect on Chromatophores*			
	Black	Red	Yellow	White
Sinus Gland	D	D	C	D and/or C
Central Nervous Organs	D	?	?	D

Key: D—Disperses
C—Concentrates

II. COLOR CHANGES OF UCA IN THE FIELD

In Table II is given a list, compiled from field observations on more than 20 species, of the apparent motivation of color changes as they occur in nature. All except those on diurnal rhythm, which have been well established by previous observers, are the result of our own field work carried out chiefly in the American tropics; they apply to a lesser extent, however, to the three northern Atlantic species mentioned above. Here only darkening and lightening are indicated, regardless of the chromatophoric principles involved.

TABLE II. COLOR CHANGE IN UCA IN THE FIELD.

Time, Place or Condition	*Crab Darkens*	*Crab Lightens*
Day	X	—
Night	—	X
Submergence in burrow	X	—
Capture and holding	X	—
Display	—	X

These color changes will be discussed in order. Since individual *Uca* show little or no adjustment to background color, that adaptation, so characteristic of many crustaceans, is not considered in the present paper.

A. *Diurnal Darkening.* It is well established that normal fiddlers are somewhat darker during the day than at night, and that this rhythm continues to a certain extent regardless of whether the crabs have been blinded, their sinus glands removed or both (see especially Abramowitz & Abramowitz, 1938, and Brown, 1944, p. 131). As mentioned above, the diurnal rhythm is probably controlled by principles from the central nervous organs, which during the day-time disperse the black pigment. As there is no evidence that the white is dispersed at night, the nocturnal lightening appears to be due to the simple concentration of the black, particularly on the legs and ventral surface. It is much less intense than the dazzling white assumed by some species in display, which often extends over the entire body and, more rarely, the appendages as well. As has long been known, *Uca* is altogether diurnal; at night it never feeds, digs or waves, and rarely even

The function of these control systems in nature has scarcely begun to be explored. Brown considers it almost certain (1944, p. 131) that the diurnal rhythm of fiddler crabs (see below), which continues to a certain extent regardless of light intensity or loss of eyes, is controlled by secretions from the central nervous organs. No function has yet been assigned, however, to the color changes controlled by sinus gland principles. In the following pages possible connections between endocrine functions and natural color change are suggested, and some aspects of the development of color in the group discussed.

ıerges from its burrow, although it may in the mouth during nocturnal low tides. day-time darkening is of conceivable actical benefit in making the crab incon- icuous in its usually dark muddy-sand or ıddy habitat.

B. *Submergence Darkening.* A fiddler ab in light display coloration (see below) darkened slowly by prolonged submersion its damp burrow. Hence the principle re- onsible for this type of darkening— ıether originating in the sinus gland, the ntral nervous organs or elsewhere—obvi- sly inhibits the effect of the display- ightening mechanism. This darkening pears more extensive than could be ex- ained merely by the saturation of the ticle and its resulting translucence, which ıuld permit body organs to show through. so, it is quite different from the superfi- al effect caused by clinging mud or sand. nce the display-brightening mechanism hibits the diurnal rhythm presumably otivated by the central nervous organs, is likely that the darkening principle of e sinus gland will be found to be respon- ble for the dispersal in burrow submer- on. Any benefit to the crab is hard to agine; it seems more likely that this ef- ct will prove to be a psychological by- oduct connected with some other process perhaps to activity of the gland in some anch of metabolism concerned with respi- tion or water-intake. In fact, this darken- g is perhaps a slight disadvantage, if, as ems almost certain, display-brightness has cognition, advertising and/or stimulating lue; a darkened crab must lose precious v tide display time in regaining bright- ss. No darkening effect is seen after brief scents, caused by momentary alarms, casional digging activities, or the need moistening the gills. It is extreme only er prolonged digging and after submerg- e during high tide.

C. *Darkening on Capture.* A similar dark- ng effect is seen when a crab in display oration is seized and held in the hand, y in this case the darkening is usually ch more rapid than when the crab merely scends into its burrow. The time required the change is highly variable in species l individuals. So far, it has appeared most id in *U. latimanus*, one of the species in ich display-blanching is most highly veloped. The incidental effect of adrenalin some vertebrate chromatophores during ergency may be kept in mind for possible rallelisms among fiddler crabs, especially view of the similarity already suspected rown, 1944b, p. 133) of crustacean cen- l nervous organ extracts to adrenalin or tylcholine. If a *Uca* nervous organ prin- le is responsible, however, for "emerg- ency" darkening of display coloration, it is probably different from the diurnal-darken- ing principle, since the latter is inhibited by the display-brightening substance.

It may be remarked here that we have not so far succeeded in inducing either dis- play-coloration or waving in any fiddlers with pronounced display colors (e.g. *U. sten- odactyla, stylifera, saltitanta,* etc.) kept in captivity, although these experiments have not yet been carried out systematically.

D. *Display Brightening.* The lightening, often to dazzling whiteness, of fiddlers in the breeding season and, during that season, of displaying individuals on bright days at low tide, has been repeatedly observed by us in both temperate and tropical species in the western hemisphere. For unknown reasons, the effect appears to reach its highest devel- opment in the tropical eastern Pacific. Its general characteristics have been previously discussed (Crane, 1941, pp. 154 ff). In re- gard to the chromatophoral hormonal as- pect, which has yet to be investigated ex- perimentally, the following remarks may be made:

1. One or more principles must be active which inhibit the normal effect of the cen- tral nervous organ principle which is appar- ently responsible for diurnal darkening as well, perhaps, as the dark-dispersing princi- ple of the sinus gland, the function of which is so far unknown.

2. The same or other principles must be responsible for the maximum dispersal of the yellow and white pigments, which are chiefly concerned in the brightening, as well as those bringing about the occasional sub- sequent concentration of the yellow (see p. 165), and special display coloration such as bright red chelae, purple ambulatories and bright blue eyestalks.

3. Since this maximum brightening oc- curs in the display season, which is inti- mately connected with breeding in at least a majority of species, it is likely that sex hor- mones, produced in the gonads or elsewhere, will be found to be responsible.

4. At least one immediate source may prove to be a dispersing-white principle of the sinus gland. The existence of this prin- ciple is recorded by Brown (1944, p. 40) as an unpublished observation, although Abramowitz (1937) has considered it as a concentrating-white agent.

5. Although no sex hormones have yet been proved to exist in Crustacea, the white chromatophores appearing in egg-bearing segments of female *Leander* should be kept in mind in attempting to explain the dis- play colors in *Uca*. Knowles & Callen (1940) found that these chromatophores failed to develop in *Leander* which had been parasit- ized or X-ray castrated, but think that little

evidence was thus given for the existence of a female sex hormone. Their preferred, alternative conclusion is that these white chromatophores are a by-product of the increased metabolic rate of the breeding season. Some such relatively simple explanation as the latter may prove to be true in *Uca*: The same authors remark on the part known to be played by guanin accumulations in the nuptial coloration of many vertebrates. Another phenomenon, reported by McVay (1942) working with *Cambarus*, may prove to have a bearing on the problem: she reports a seasonal change in the concentration of the white chromatophore-contracting principle from the brain of females, and a striking difference between males and females in the total amount present. It is likely that the seasonal behavior of white pigment in the three crustaceans—shrimp, crayfish and fiddler crab—will prove to be related. Should a basic execretory origin be proven, an adaptive use of the resultant white pigment as a recognition and stimulatory device in *Uca* would not of course be necessarily eliminated.

Some further aspects of display-brightening are considered in the following section.

III. Development of Display Color.

A. *Sequence of Display Color Development.* In individuals as well as in the apparent trends of evolution within the genus, a certain sequence of chromatophoral display color development is discernible. This runs from black to red to yellow to white. When each of these colors appears dominant, obviously the pigment within the remaining chromatophores is concentrated. The full course of this black-white change is seldom run, and one or more phases are usually suppressed, but in various stages it can be traced in both groups of species and in individuals within a species. Also, save for some exceptions in the development of color on major chelipeds, the sequence never changes: for example, a white carapace never precedes a yellow, nor yellow legs red. Combination phases of orange, pink and cream in various stages of development occur frequently, however, and must be brought about by the simultaneous dispersal of red and yellow, red and white, and yellow and white pigment, respectively.

The fifth pigment, blue, which has been shown in other crustaceans to be extra-chromatophoric, is relatively uncommon and behaves irregularly. It is almost always confined to local areas, such as eyestalks, mouthparts or frontal regions. It may be said here only that it is a true display color, developing at the expense of diurnal black, and inhibited both by burrow submergence and by capture. It seems always to develop before the general dispersal of white, and usually persists even when white has succeeded the remaining pigments. Often it has a strongly iridescent appearance, and may range in shade from purple and violet to turquoise and green, doubtless through simultaneous expansion of red or yellow chromatophores, respectively.

The behavior of the chromatophoric pigments will now be considered from other angles

B. *Display White as an Evolutionary Trend.* In a previous paper (1941, p. 156) it was pointed out that dazzling white is exceedingly prevalent in the display coloration of the end-forms in each of the three groups of *Uca* in which display had at that time been observed. This white is assumed seasonally by the species, and daily by the individuals. Typical examples of this extreme whitening are *stylifera* in Group 1, *saltitanta* in Group 4 and *terpsichores* in Group 5. Since then, I have had opportunities of noting display coloration in a number of Group 2 fiddlers (examples: *pugnax, mordax*) as well as in other examples of the remaining groups, and have found no reason to alter the conclusion that the development of display-white is a general evolutionary trend throughout the genus. It is most common in the widely separated Groups 1 and 5, which contain the most specialized species, moderately so in Group 4, and rarest in Group 2; it is also well developed in 6, the offshoot proposed for the aberrant *panamensis* (*l.c.*, p. 166). Occurrence in Group 3 has not yet been studied.

Group 2 continues to appear to be the most primitive western hemisphere group, and, as just noted, white is less highly developed here than in any of the others. An exception is *galapagensis*, a close Pacific relative of *pugnax*; when seen in display, in Ecuador, 1944, the few waving examples were pure white; all the rest, both males and females, ranged from grayish to bright yellow and cream.

Depending on the sequence and extent of lightening of carapace in display coloration, species in which this phenomenon has been carefully observed may be divided into five divisions, as follows:

(a). Dark: No appreciable yellowing or whitening of carapace; display colors confined chiefly to appendages. Group 1: *maracoani, insignis;* Group 4: *oerstedi, spinicarpa, inaequalis, batuenta, cumulanta.*

(b). Carapace changes from dark to muddy yellow or grayish-white: Group 2: *pugnax, mordax, minax;* Group 4: *festae.*

(c). Carapace changes from dark to cream: Group 5 (primitive offshoot), *pugilator.*

(d). Carapace changes from dark to pink to white: Group 5, *stenodactyla* (but bright blue maintained anteriorly).

(e). Carapace changes from dark to yellow to cream to white: Group 1, *stylifera, princeps;* Group 2, *galapagensis.*

(f). Carapace changes from dark to cream to white: Group 4, *saltitanta;* Group 5, *beebei, deichmanni, terpsichores, latimanus;* Group 6, *panamensis.*

Several points must be emphasized here: First: the above represents *maximum* known color changes for each species. Sometimes, as in the case of *princeps* and *beebei* (see p. 166), they are not attained in every population. Sometimes, as in *pugnax,* dark displaying crabs are the rule, and lighter phases the exception. Contrariwise, individual crabs will be found displaying, or even actually mating, in colors not nearly as bright as those characterizing their immediate neighbors. Finally, (f) differs from (e) only in having the white pigment start diffusion simultaneously with, instead of subsequent to, the yellow.

Dispersal of red and yellow pigment often persists simultaneously with black, as may be seen by the persistence of red joints in *U. minax* apparently at all seasons, and of the frequent occurrence of reddish-or-yellowish-brown carapaces, as well as of ochraceous tinges on the chelipeds, even when some species are in their dark phases. Pure yellow and cream phases are exceedingly transitory, however, and require special comment. In at least the three species listed under (e) above, the adults, both males and females, of whole populations coming into the display season go for days, perhaps weeks, with daily changes to the bright yellow, or at most cream-yellow phase, but no continuation into white—that is, no subsequent concentration of yellow pigment accompanied by full dispersal of white. Later, individuals of *princeps* and *stylifera* have been seen to skip the yellow altogether in the daily change. Whether entire populations at the height of the breeding season may skip the yellow is not yet known. However, in the species listed under (f) above, which are preponderantly of the specialized Group 5, the creamy daily phase is sometimes so short as to be practically nonexistent, or it may be confined to some yellow speckles on the carapace, giving an over-all cream appearance.

To account for these phenomena, four separate chromatophoric actions must be explained, even when the frequent involvement of red and blue pigment is omitted: (1), The normal diurnal expansion of the black pigment is inhibited; (2), the yellow pigment is dispersed; (3), the yellow pigment is concentrated; (4), the white pigment is dispersed. Whether a separate hormone is responsible for each mechanism is of course completely unknown. Equally unknown is whether these chromatophoral changes are merely by-products of physiological processes concerned in reproduction, whether they are a true adaptive result of display evolution, with recognition and/or stimulatory functions, or whether temporary intermediate phases, such as the yellow, are recapitulations of ancestral conditions. All three possibilities will probably be found to be true in part, and to vary with the species. Brown and Wulff's (1941, p. 344) observations on the behavior of yellow pigment in *Crago* should be kept in mind: the yellow in eyestalkless animals was first maximally concentrated and then rapidly dispersed by sinus gland extracts.

C. *Example of Color Development: U. princeps.* The large cheliped and often the ambulatories may run a course of color development independent of that of the carapace. For example, a majority of even the dullest fiddlers have the tips of the chelae completely white, and a great deal of red or orange at least on the major manus, while purple shades are common on the ambulatories. This red or orange sometimes persists even in species which otherwise change the carapace to complete white (example: *stylifera*). Again, the dispersed pigment of the cheliped may not only persist but may be white in the young, and reverse the usual sequence by developing orange and red secondarily, as shown below.

An example of ontological color development will be given in detail, as it occurs in *U. princeps,* which passes through a distinct yellow phase. The observations were all made at Puerto Bolivar, Ecuador, late in April. Apparently the display season was just beginning.

Stage I. up to *ca.* 10 mm. Carapace above and below greenish-brown; manus and chelae brilliant white, inside and out; ambulatories rich plumbaceous anteriorly; rest of cheliped and other legs muddy brown; eyestalks green or greenish-yellow. One exception, among hundreds of similar size, showed precocious coloration, being entirely white.

Stage II. ca. 11 to 18 mm. Like above, except for yellow developing on lower part of manus. This changes to dull orange, then blazing scarlet orange and spreads all over manus, inside of carpus and merus and throughout pollex except tip.

Stage III. ca. 19 mm. to maximum (*ca.* 30 mm.). Cheliped remains bright; carapace and legs lighten to dull orange.

Stage IV. Like above, except dull orange carapace and legs brighten to yellow, then cream. A few males in this stage fought and

displayed. This was the most abundant stage among adults, which obviously were not in full display season.

Stage V. Crab completely dazzling white except for bright orange pollex, or pollex and lower manus. All the males in this stage were displaying.

D. *Sexual Dimorphism*: As in many other groups of animals, there are species of *Uca* (e.g. *saltitanta, stenodactyla, latimanus*) where the female is always very dull and the male exceptionally brilliant in display coloration, while in closely related species the females are as bright as the males (except, of course, for absence of the often gaudily colored major cheliped). The latter group includes some species where white development reaches its height. The most striking examples of this found to date are the females of *princeps* and *terpsichores*, all observed in Ecuador. In others, such as *galapagensis* and *pugilator*, the female attains a cream only slightly deeper than the white or cream of the male. It may be noted that in species such as *stenodactyla*, where the female is very dull and the male especially bright, the dimorphism in size is also extreme; in those where the color difference is slight, the size difference also is relatively small. Here is another possible example of linked hormonal effects.

E. *Geographic Color Variation*: A most interesting observation made in Puerto Bolivar, Ecuador, gives evidence of marked geographic variation in the display colors of two species. Study of displaying *princeps* (Group 1) and *beebei* (Group 5) in Panama (February and March, 1941) during the dry season (1941, pp. 170, 193) showed that these species, although waving strongly, and with ovigerous specimens present, showed practically no white except on the fingers: instead, the display coloration consisted of gray, rose, orange and purple in *princeps* (which were in Stage II., p. 165), and gray, green, purple and ochre in *beebei*. Close relatives of each, on the other hand, *stylifera* and *terpsichores*, respectively, when in full display coloration had everything except the appendages dazzling white.

In observations made in April, 1944, at Puerto Bolivar, Ecuador, displaying individuals of both *princeps* and *beebei* were found to be almost completely dazzling white in color, although individuals of the darker and intermediate shades were present, as usual. In *princeps* there was also, as described above, an intermediate yellow phase. In *beebei*, a very few individuals in the darker phase characteristic of Panama were displaying; in *princeps*, none.

It was near the beginning of the dry season in Ecuador, so that the comparison with the Panamanian observations was ideal. In morphological characters the individuals proved typical of their species in every detail, and their displays were indistinguishable. More evidence that the variation is actually geographic, and not a result of the observations of purely season differences, lies in the fact that immediately after the Ecuadorian study, the same Panamanian mud-flats at La Boca, Canal Zone, and Bellavista, Panama City, were visited during the second week in May, after the start of the rains. Both species were displaying, and both were in the identical dark coloration found three years previously during the dry, without a single white individual present, even on the clearest, sunniest days at full low tide.

A point of special interest concerns the size difference between displaying males of *princeps* in the two regions. In 1941 (p. 70) it was remarked that in the Panamanian colonies the largest males seen, all of which were displaying strongly, measured around 15 mm. in length, although the maximum measurements of specimens from other localities were around 25 mm. In addition, it has been determined that in these small males the abdominal appendage is slightly pre-adult in form. The same conditions prevailed there in 1944 in the colony at Puerto Bolivar; however, the only males displaying were large individuals measuring around 25 to 30 mm., with abdominal appendages of mature development, and all of these were in the white, or at least the creamy-yellow phase. As far as could be determined, general ecologic factors were exceedingly similar; in both the Panamanian and Puerto Bolivar populations, the salinity (high tide, near full moon: unfortunately only one sample was taken from each) was about 38 parts per thousand, or about 75 per cent. of average open ocean concentrations; also, the general facies of the mud-flats, including high Pacific tides, and climatic conditions with pronounced wet and dry seasons, were much alike.

There are at least four possible explanations, which are not necessarily mutually exclusive.

(1). In the Panamanian habitat some unknown environmental factor may promote early maturation of the sex glands before maximum size and pigment development are attained.

(2). Contrariwise, a factor may inhibit development of the last two characteristics.

(3). In Puerto Bolivar, some factor may encourage the production of white and yellow pigment, or of the hormone(s) governing their dispersal, or both. Since the white is confined to displaying forms, however, connection with gonad activity still seems essential. Also, this alternative would no

be adequate to explain the small size and pre-adult form of abdominal appendages in Panamanian *princeps*. It would however be sufficient to cover the development of the white in Ecuadorian *beebei*, which show no size or appendage difference from Panamanian specimens.

(4). A fourth explanation, which would apply equally well to both species, is that in Puerto Bolivar species development, through mutation and selection, has progressed beyond the stage found at Panama, and has reached the normal summit of *Uca* color evolution, which tends toward white display dress in all groups.

Because of the lack of morphological differences and the presence of Panamanian color phases in both *princeps* and *beebei* at Puerto Bolivar among the white individuals, there seems to be no adequate basis at present for the erection of subspecies or other subdivisions. The same two species must obviously be studied in other localities and at all seasons before the "normal" forms can be identified.

F. *Ecologic Factors*: Too little is known of precise ecological factors to draw any conclusions at present. It may only be stated here that so far as known crabs with the most brilliant coloring, including development of display white, live only on tropical shores with more than half the salt concentration of open ocean water and a high tidal range. In the western hemisphere, these conditions are met in the tropical eastern Pacific, where the most active species, and the greatest numbers of species also occur. Second, bright sun is needed to bring about maximum dispersal of white pigment, just as it is necessary for maximum display activity: although there are always individual exceptions, a given population is invariably notably darker and far less active on cloudy days than on clear.

IV. Summary and Conclusions.

Four types of normal color changes in *Uca* have been described, namely diurnal darkening, submergence darkening, darkening on capture and display brightening. None except the first has been studied microscopically or investigated experimentally from an endocrinal viewpoint. It is already fairly certain that diurnal darkening is brought about by a secretion from the central nervous organs; it is suggested in the present paper that the slow-working submergence darkening may be motivated by the dark-dispersing element of the sinus gland, while the relatively rapid darkening on capture may be controlled by the latter, or by another element in the nervous organs. The display brightening principle(s) inhibit the diurnal darkening mechanism as well as the normal sinus gland darkening, and are in turn inhibited by those of the submergence and capture darkening.

Display brightening includes, in addition to widely occurring bright chelipeds and ambulatories in males, a general trend throughout the genus toward the development of complete dazzling whiteness in both sexes during the display season. Fully white crabs occur in widely separated species. In ontological seasonal and daily changes, a strict sequence of display color development is apparent, which runs from black to red to yellow to white, each phase representing dispersal of one of the four chromatophoric pigments. Any of the phases except the first may be suppressed, and combinations are frequent, giving orange, pink and cream effects. Yellow and cream phases are the most transitory. In most but not all species where bright display color is well developed, the carapaces of the females are decidedly darker than those of the males. Two cases of geographic color variation are described, where displaying males of two unrelated species are dazzling white in Ecuador and much darker in Panama, under apparently similar ecological conditions. In one species, the dark Panamanian examples, although giving all signs of actual breeding, were in addition small with subadult abdominal appendages.

Ecologic factors for development of display color have not yet been specifically studied. Bright sun, however, is essential for maximum daily development of display color. So far, the brightest and most active of western hemisphere species, as well as the greatest local concentration of species, have been observed in the tropical eastern Pacific on shores with high tidal ranges and with a salinity concentration of more than half that of open ocean water.

The above data has been put on record with the chief hope of suggesting lines for future endocrine and psychological research in this group, preferably with a combination of field and laboratory methods. The adaptive functions of display color are still only suspected: it is not even known whether fiddler crabs have color vision, much less whether the brightening of the male crab in display has recognition and/or stimulating value for the female, and serves for territorial limitation and challenge to other males, whether it is merely a metabolic by-product, or whether recapitulation of ancestral color is involved in cases of transitory phases. Judging from the behavior of the females and rival males, however, it seems certain that at least the brightness (irrespective of color) of the waving chelae,

which adds so much to the conspicuousness of the display in even the dullest species, must be of actual value.

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